

## MICROHABITAT DISTRIBUTION OF TWO FLORIDA SCRUB ENDEMIC PLANTS IN COMPARISON TO THEIR HABITAT-GENERALIST CONGENERS<sup>1</sup>

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Habitat-specialist species may be restricted to a narrower range of microhabitats than habitat-generalist species. We addressed this hypothesis by comparing microhabitats of two pairs of congeners that differ in habitat specificity and co-occur in one distinct habitat type, Florida rosemary scrub. We characterized microhabitats of rosemary scrub specialists, *Polygonella basiramia* and *Lechea cernua*, their habitat-generalist congeners, *Polygonella robusta* and *Lechea deckertii*, and random points in the rosemary scrub habitat. Plants of both habitat specialists occurred in microhabitats with significantly more bare sand than plants of habitat-generalist species and random points. Plants of all four species occurred in microhabitats that were farther from dominant shrubs, *Ceratiola* and *Quercus* spp., than random points. Seedlings of both habitat specialists grew larger in bare sand microhabitats, whereas ground lichens and litter did not affect seedling growth of the habitat generalists. As the time since fire increases, bare sand cover decreases, *Ceratiola* density increases, *Quercus* density remains constant, and shrubs become taller. Physical characteristics, such as soil temperature, soil carbon, and soil moisture, differ slightly with respect to microhabitat. Our results suggest that *P. basiramia* and *L. cernua* are specialized on bare sand microhabitats that characterize their preferred habitat, rosemary scrub. Microhabitat specialization may limit the distribution of these rare species.

**Key words:** congeneric species-pairs; Florida scrub; habitat specialization; *Lechea*; microhabitat; *Polygonella*; rarity; rosemary scrub.

Habitat specialization is widely cited as a potential cause of rarity (Vivian, 1967; Kruckeberg and Rabinowitz, 1985; Hodgson, 1986; Hubbell and Foster, 1986; Buchele et al., 1989; Prober and Austin, 1990) and species coexistence (Bazzaz, 1991; Clark et al., 1993; Debski et al., 2002); however, the mechanistic basis of habitat specificity is often not well understood. Species that persist in only a small subset of habitat types within a given geographic area are considered habitat specialists. Strong and consistent selection imposed by environmental conditions characteristic of the preferred habitat(s) is predicted to cause habitat specialization (Bazzaz, 1991).

The key to understanding ecological phenomena such as habitat specialization depends on the clarification of mechanisms behind observed distributions and identification of the scale at which these mechanisms function (Levin, 1992). The definition of commonness and rarity is scale dependent (Schoener, 1987); there are several different types of rarity defined by geographic regional abundance, local abundance, and habitat specificity (Rabinowitz, 1981). Seemingly contradictory models describing patterns of abundance are compatible when the scales referred to in each model are considered (Collins and Glenn, 1991). In certain cases, studies that focus on large spatial scales may be hampered by neglecting smaller

scales, which often may be more relevant to mechanisms causing observed distributional patterns (Huston, 1999).

The difference between habitat and microhabitat is a difference of scale, and we argue that this distinction is critical to the elucidation of the mechanisms underlying the restriction of rare, habitat-specialist plants. Habitat generally refers to strong environmental discontinuities at large scales, greater than 10<sup>3</sup> m (Svenning, 1999) and is usually characterized by the dominant plant forms or physical characteristics of the habitat (Ricklefs, 1990). Microhabitat refers to environmental conditions that vary at small scales (Svenning, 1999) and can be defined as the environmental conditions surrounding an individual (Menges et al., 1999).

Habitat generalists and habitat specialists are expected to differ in their response to variation in microhabitat. Generalists that can occupy several habitat types are predicted to exhibit little difference in performance among habitat types (Seamon and Adler, 1996) and little specificity for particular microhabitats within a single habitat type (Brown and Pavlovic, 1992). Conversely, the performance of specialists that are restricted to a single habitat may be dependent on particular microhabitat conditions that are characteristic of their preferred habitat (Rosenzweig, 1981). Thus, the performance of habitat specialists may be differentially affected by contrasting microhabitat types within a habitat (Griffith, 1996; Hilton and Boyd, 1996; Menges and Kimmich, 1996; Kephart and Paladino, 1997; Dinsdale et al., 2000; Wolf, 2001; Bruno, 2002; Colling et al., 2002).

A variety of mechanisms have been proposed as causes of habitat specialization. Regeneration niche specialization (Hubbell and Foster, 1986), narrow physiological tolerance (Robson and Maze, 1995), and poor competitive ability (Griggs, 1940) are among the leading causes suggested for habitat specialization. Each instance of specialization may be caused by any

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of these factors alone or in combination; however, specialization should be measured relative to other related species (Futuyma and Moreno, 1988).

Comparison of congeneric rare and common species can be a useful approach to understanding rarity (Bevill and Louda, 1999) and ecological specialization (Futuyma and Moreno, 1988). Such comparisons may provide insights into the relative importance of various ecological factors that affect population persistence (Fiedler, 1987; Prober, 1992; Byers and Meagher, 1997; Menges et al., 1999). The comparison of close relatives minimizes the chance that observed differences may be artifacts of phylogenetic inertia. However, consideration of ecological criteria, such as preferred habitat types of each species, is also important in selecting appropriate species-pairs for comparison because it minimizes the potentially misleading effects of contrasting ecological forces on differences in life history (Bevill and Louda, 1999). In this study, we compare congeners that occur sympatrically, in at least some of the same habitat patches. Specifically, we compare the microhabitat utilization of two habitat-specialist species with their habitat-generalist congeners, in the habitat where they co-occur.

We tested the hypothesis that habitat specialists occur in a narrower range of microhabitat conditions within a habitat than species that occur in a larger number of habitats. We compared microhabitats of two rare species that are restricted predominantly to Florida rosemary scrub habitat with congeners that co-occur in rosemary scrub but also commonly occur in other habitats. We also analyzed microhabitats of all species in comparison to random points in rosemary scrub habitat to evaluate the importance of various microhabitat variables to the distribution of both specialist and generalist species in rosemary scrub habitat. In addition, we investigated the potential mechanisms behind differences in microhabitat utilization of habitat specialists and generalists with a series of experimental and observational studies. We compared seedling survival and growth of habitat specialists and generalists in contrasting microhabitats, testing the hypothesis that habitat specialists may have a narrower regeneration niche than habitat generalists. We also characterized the abiotic properties of microhabitats, to determine if soil temperature, soil nutrients, and soil moisture differed consistently across contrasting microhabitats in a way that could explain narrower physiological tolerance of habitat specialists to particular microhabitat conditions than habitat generalists.

## MATERIALS AND METHODS

**Study species**—We characterized the microhabitat preferences of two congeneric pairs of species. All four species are short-lived, perennial, suffrutescent herbs (Wunderlin, 1982). One member of each congeneric pair is a Florida scrub endemic. *Polygonella basiramia* (Small) Nesom and Bates is endemic to the Lake Wales Ridge and the Avon Park Bombing Range Ridge (Christman and Judd, 1990). *Lechea cernua* Small occurs patchily throughout the Lake Wales Ridge and the scrubs of peninsular Florida, USA (Christman and Judd, 1990). Both of these endemic species are restricted predominantly to large white-sand gaps in Florida rosemary scrub (Christman and Judd, 1990; Hawkes and Menges, 1995; Anonymous, 1999). The other member of each pair is more widespread. *Polygonella robusta* (Small) Nesom and Bates occurs in sandy habitats throughout Florida, and *L. deckertii* Small occurs in sandy habitats throughout Florida and southern Georgia (Wunderlin, 1982). Both of these more widespread species also have more general habitat requirements, occurring in other sandy habitats, such as scrubby flatwoods and sandhills, in addition to co-occurring in Florida rosemary scrub (Wunderlin, 1982; Abrahamson et al., 1984).

**Study site**—This study was conducted at Archbold Biological Station (ABS), a 2000-ha private biological station in Highlands County, Florida. Annual rainfall exceeds 1200 mm, with the majority falling in June through September due to convective thunderstorms and tropical storm systems (Abrahamson et al., 1984; Menges, 1999). A variety of habitats are found at ABS, including approximately 36 ha of rosemary-phase sand pine scrub, or “Florida rosemary scrub,” the preferred habitat of the habitat-specialist species in our study (Abrahamson et al., 1984). Florida rosemary scrub is dominated by the shrub Florida rosemary, *Ceratiola ericoides* Michx., which occurs in pure stands or intermixed with scrub oaks (*Quercus inopina* Ashe, *Q. chapmannii* Sarg., and *Q. geminata* Small) and sand pines [*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg.] (Abrahamson et al., 1984). This low-productivity ecosystem is located on nutrient-poor, excessively drained, xeric white sands—entisols of the St. Lucie or Archbold series (Abrahamson et al., 1984; Carter, 1999). Fire-return intervals in rosemary scrub average between 15–60 yr (Menges, 1999). *Ceratiola ericoides* is killed by fire and recovers via seedling establishment (Johnson and Abrahamson, 1990). Most other shrubs in rosemary scrub, predominantly *Quercus* spp., recover rapidly from fire by resprouting (Abrahamson, 1984b; Schmalzer, 2003). *Ceratiola ericoides* and *Quercus* spp. form the boundaries of bare sand gaps in rosemary scrub (Menges, 1999). Periodic fires aid in maintaining open-structured habitat with large bare sand gaps that are distinguished from the surrounding shrub matrix by the lack of large *Ceratiola* shrubs, and lower levels of leaf litter and ground lichens (Menges, 1999). Several herbaceous plants are specialized on these bare sand gaps (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernandez, 1997; Menges and Hawkes, 1998; Petru and Menges, 2003).

**Microhabitat characterization**—We characterized the microhabitats surrounding individual plants of each species relative to randomly chosen points within rosemary scrub. We measured microhabitat variables for randomly selected plants from each of six populations of *L. cernua* ( $N = 551$ ), *L. deckertii* ( $N = 536$ ), and *P. basiramia* ( $N = 523$ ), and each of five populations of *P. robusta* ( $N = 369$ ). For *L. cernua*, *L. deckertii*, and *P. basiramia*, two populations were selected from rosemary scrub patches in each of three time-since-fire classes: recently burned ( $<5$  yr), intermediate-aged (12–15 yr), and long-unburned ( $>25$  yr). For *P. robusta*, two populations were selected in each of the intermediate-aged and long-unburned time-since-fire classes, but only one population in the recently burned class was included in this study. In most cases the same rosemary scrub patch contained all or most of the study species. Nine sites were used in this study—three sites in each of the three time-since-fire classes. At each of these nine sites, we also randomly selected 50 points within regions of the rosemary scrub patch that contained plants of at least one of the study species. We compared the microhabitats of random points in rosemary scrub habitat of the three time-since-fire classes to determine how microhabitat characteristics change with duration after fire.

Microhabitat was defined as the area within a circular quadrat of 27 cm radius (area of 0.229 m<sup>2</sup>) centered on the randomly selected plant or point. For each plant or point, we visually estimated the percentage cover of open sand to the nearest 10% and measured the maximum height to the nearest 10 cm of the nearest shrub greater than 50 cm in height. We also measured the distance to the nearest 10 cm from the nearest *Ceratiola* and *Quercus* spp. greater than 50 cm in height.

**Seedling experiment**—We manipulated the lichen and litter microhabitats of naturally established seedlings of all four study species in two rosemary scrub habitat patches; *L. cernua* and *L. deckertii* seedlings were together in one patch, and *P. basiramia* and *P. robusta* were together in the other. In the first week of June 2002, we randomly selected 50 seedlings of each species and measured initial height for each seedling. Initial heights of seedlings ranged from 2–5 cm. We then randomly assigned 25 seedlings of each species to each of two different microhabitat treatments. A bare sand treatment was applied by removing all lichens and litter in a 25-cm radius around a target seedling, and a lichen and litter treatment was applied by adding lichens and litter to attain 100% coverage and 1–2 cm depth in a 25-cm radius around a target seedling. At the beginning of November 2002, we measured final height, crown diameter, and crown width (the horizontal distance perpendic-

ular to crown diameter). We estimated final size by calculating volume of an inverted cone (tapering from maximum diameter at the top of plant to a point) using these measured variables.

**Physical characterization of microhabitats**—We characterized the physical properties of contrasting microhabitats with a series of both experimental and observational studies. We conducted a soil temperature experiment to determine the effect of lichen and litter cover and distance from nearest *Ceratiola* on soil temperature. We also conducted soil nutrient and soil moisture studies to determine how levels of carbon, nitrogen, and moisture in the soil differed with respect to microhabitat and time-since-fire.

During a 7-d period at the end of October 2002, we measured soil temperature at 15-min intervals in four different microhabitat treatments within rosemary scrub habitat using portable HOBO dataloggers with internal temperature sensors (ONSET Computer Corporation, Pocasset, Massachusetts, USA). We designed microhabitat treatments as a factorial combination of the lichen and litter treatment and distance from *Ceratiola*. We created two levels of the lichen and litter treatment (lichens and litter added in 100% coverage and 1–2 cm depth vs. lichens and litter removed to expose 100% bare sand), and two levels of distance to nearest *Ceratiola* (under the dripline on the N side of a *Ceratiola* >50 cm tall vs. > 2 m from any *Ceratiola* >50 cm tall). For each of the four different microhabitat treatments, we used one datalogger in each of five replicate microhabitat treatment locations to measure soil temperatures. We placed sensors 0.5 cm below the soil surface and replaced lichens and litter to 100% cover on top of the buried sensors for those treatments with lichen and litter cover. To determine the effects of each treatment on soil temperature, we compared means of the absolute maximum temperature and absolute minimum temperature for each treatment during the 7-d period.

In February 2003, we collected soil samples from four different microhabitats and two different times since fire and sent subsamples to Oregon State University's (OSU) Central Analytical Laboratory to be measured for total C and N using a Leco CNS-2000 Macro Analyzer (Leco Corp., St. Joseph, Michigan, USA). We collected samples from two sites each in two different time-since-fire categories: long-unburned (>30 yr since last fire) and recently burned (<2 yr since last fire). At long-unburned sites, we sampled three replicates each of four different microhabitat types. We defined four microhabitat types: (1) >90% bare sand, >2 m from any *Ceratiola* >50 cm, and >1 m from any *Quercus* >50 cm; (2) >90% lichen and litter cover, >2 m from any *Ceratiola* >50 cm, and >1 m from any *Quercus* >50 cm; (3) under the dripline of a *Ceratiola* >50 cm tall; and (4) under the dripline of a *Quercus* >50 cm tall. At the recently burned sites, we only were able to locate and sample microhabitat types 1 and 4. At each site, we randomly sampled three replicates for each microhabitat type. For each microhabitat sampling location, we removed two soil samples 7 cm in diameter by 5 cm deep which were then combined and homogenized. One 5-g subsample was removed from each sample, and subsamples were packaged in Ziploc bags and sent to OSU for analysis within 24 h of collection.

In May 2003, we measured soil moisture gravimetrically with soil samples collected from four different microhabitats and two different levels of time-since-fire. We collected samples from the same sites, in the same time-since-fire categories, and using the same microhabitat type definitions described above. At each site, we randomly sampled five replicates for each microhabitat type. For each microhabitat sampling location, we removed and combined two soil samples 7 cm in diameter by 5 cm deep. We weighed the samples immediately after collection, then dried them for 24 h at 37°C and weighed them again. We calculated soil moisture as percentage of dry mass.

**Data analysis**—All data were analyzed using The SAS System for Windows, version 8.02 (SAS Institute Inc., Cary, North Carolina, USA). Microhabitat data were not normally distributed and could not be transformed to normality. We summarized the frequencies of plants and random points for each level of each microhabitat variable and generated cumulative percentage frequency distributions. We conducted Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf, 1995) of pairs of distributions of each microhabitat variable. For each congeneric pair, we compared the distributions of each species and

compared each species with random points. For the random point data only, we conducted Kruskal-Wallis tests (PROC NPAR1WAY) for mean differences between each pair of the three time-since-fire categories. In both the Kolmogorov-Smirnov and the Kruskal-Wallis tests, we adjusted  $\alpha$  for the three comparisons made by using the Bonferroni correction, resulting in  $\alpha = 0.017$ . Seedling survival data were analyzed by species using logistic regression (PROC LOGISTIC) with microhabitat treatment and initial height as explanatory variables. Seedling size data were normally distributed, and we compared treatment means of final seedling size by species with ANOVA using general linear models (PROC GLM). Soil temperature, soil carbon, and soil moisture data were also normally distributed; therefore, we compared means with ANOVA using general linear models (PROC GLM) and tested for differences between multiple means using the Tukey-Kramer adjustment.

## RESULTS

**Microhabitat effects on plant distribution**—Rosemary scrub specialists, *L. cernua* and *P. basiramia*, occurred in microhabitats with significantly more bare sand than their habitat-generalist congeners and more than twice the cover of bare sand as random points (mean = 82% for *L. cernua*, 85% for *P. basiramia*, 54% for *L. deckertii*, 47% for *P. robusta*, 38% for random points). For both rosemary scrub specialists, over 70% of all individuals sampled occurred in microhabitats with  $\geq 80\%$  bare sand (73% for *L. cernua* and 80% for *P. basiramia*), whereas only 36% of *L. deckertii* individuals and 29% of *P. robusta* individuals occurred with  $\geq 80\%$  bare sand (Fig. 1A and 1B). The distributions of the generalist congeners are not as skewed towards the highest levels of bare sand as are those of the rosemary scrub specialists (Fig. 1A and 1B, Table 1). The striking restriction of the rosemary scrub specialists predominantly to microhabitats with  $\geq 80\%$  bare sand can also be illustrated by their relatively small coefficients of variation (CV) for percentage bare sand (CV = 27.9 for *L. cernua*; CV = 24.7 for *P. basiramia*). The coefficients of variation for percentage bare sand of the habitat-generalist congeners are much higher (CV = 59.8 for *L. deckertii*; CV = 72.6 for *P. robusta*).

Plants of all four species were farther from *Ceratiola* than random points, but rosemary scrub specialists, *L. cernua* and *P. basiramia*, were not consistently farther from *Ceratiola* than their generalist congeners. *Lechea deckertii* was less likely than random points to occur within 320 cm of *Ceratiola*, followed by *L. cernua*, (less likely within 210 cm), *P. basiramia* (less likely within 180 cm), and *P. robusta* (less likely within 110 cm) (Fig. 1C and 1D). Fewer plants of *P. basiramia* occurred near *Ceratiola* than plants of *P. robusta* (Fig. 1D), but the distance from *Ceratiola* did not differentially affect the distributions of *L. cernua* and its generalist congener (Fig. 1C).

Three of four species (*L. cernua*, *P. basiramia*, and *P. robusta*) occurred less frequently near *Quercus* than random points, but the rosemary scrub specialists were not consistently farther from *Quercus* than the habitat generalists. *Lechea cernua* was less likely than random points to occur within 180 cm of *Quercus*, followed by *P. robusta* (less likely within 170 cm), and *P. basiramia* (less likely within 130 cm) (Fig. 1E and 1F). Fewer plants of *L. cernua* occurred near *Quercus* than plants of *L. deckertii* (Fig. 1E), but distance from *Quercus* did not differentially affect the distributions of *P. basiramia* and its generalist congener (Fig. 1F).

The nearest shrub height was not correlated with the distributions of any of the four species. The nearest neighboring shrubs of the rosemary scrub specialist, *Lechea cernua*, were

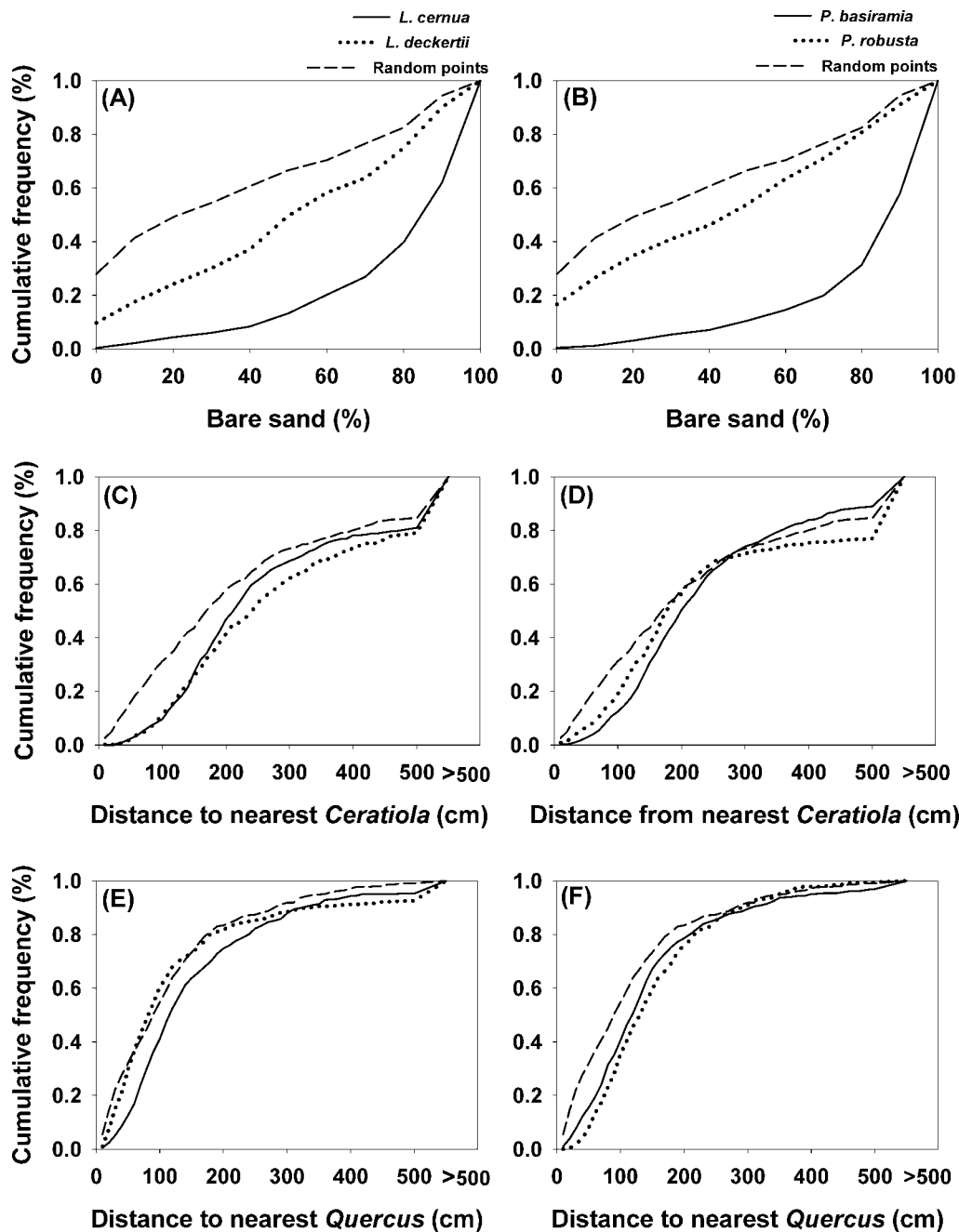


Fig. 1. Cumulative frequency distributions of (A, C, E) both *Lechea* species and (B, D, F) both *Polygonella* species compared to random points in rosemary scrub habitat for three microhabitat variables: (A, B) percentage bare sand, (C, D) distance to nearest *Ceratiola*, and (E, F) distance to nearest *Quercus* spp. Data for rosemary scrub specialists, *L. cernua* and *P. basiramia*, are depicted with solid lines, habitat generalists, *L. deckertii* and *P. robusta*, with dotted lines, and random points with dashed lines. Kolmogorov-Smirnov tests are shown in Table 1.

slightly shorter than those of its generalist congener (mean = 82 cm for *L. cernua*, 86 cm for *L. deckertii*), but neighboring shrub height did not differentially affect the distributions of *P. basiramia* and its generalist congener (Table 1). *Lechea cernua*, *L. deckertii*, and *P. basiramia*, did not occur near shorter shrubs than those near random points; however, nearest neighboring shrubs of the habitat generalist, *P. robusta*, were somewhat shorter than those near random points (mean = 84 cm for *P. basiramia*, 76 cm for *P. robusta*, 87 cm for random points) (Table 1).

**Microhabitat effects on seedlings**—Although bare sand was an important determinant of the distributions of the rosemary scrub specialists, and the habitat generalists to a lesser degree, seedlings were not consistently affected by soil surface microhabitat treatments. Seedling survival was not affected by the soil surface microhabitat treatment for three out of four species (Fig. 2, Table 2); however, for *P. basiramia*, seedling survival was higher in lichen and litter covered microhabitats than bare sand microhabitats (Fig. 2C, Table 2). Final seedling size was not affected by the soil surface microhabitat treatment for *L.*

TABLE 1. Results of Kolmogorov-Smirnov tests between pairs of cumulative frequency distributions of four microhabitat variables for *Lechea cernua*, *L. deckertii*, *Polygonella basiramia*, *P. robusta*, and random points in rosemary scrub habitat. Distributions that are significantly different at  $P = 0.017$  are designated with asterisks. Cumulative frequency distributions are shown in Fig. 1 for all variables except height of nearest shrub.

Microhabitat variable	Comparison	$D_{\max}$	$D_{\max} > D_{\alpha}$
Percentage bare sand	<i>Lechea cernua</i> $\times$ random points	0.533	*
	<i>L. deckertii</i> $\times$ random points	0.250	*
	<i>L. cernua</i> $\times$ <i>L. deckertii</i>	0.381	*
	<i>Polygonella basiramia</i> $\times$ random points	0.567	*
	<i>P. robusta</i> $\times$ random points	0.148	*
	<i>P. basiramia</i> $\times$ <i>P. robusta</i>	0.511	*
Distance from nearest <i>Ceratiola</i>	<i>L. cernua</i> $\times$ random points	0.216	*
	<i>L. deckertii</i> $\times$ random points	0.203	*
	<i>L. cernua</i> $\times$ <i>L. deckertii</i>	0.101	*
	<i>P. basiramia</i> $\times$ random points	0.188	*
	<i>P. robusta</i> $\times$ random points	0.128	*
	<i>P. basiramia</i> $\times$ <i>P. robusta</i>	0.120	*
Distance from nearest <i>Quercus</i>	<i>L. cernua</i> $\times$ random points	0.196	*
	<i>L. deckertii</i> $\times$ random points	0.072	
	<i>L. cernua</i> $\times$ <i>L. deckertii</i>	0.197	*
	<i>P. basiramia</i> $\times$ random points	0.172	*
	<i>P. robusta</i> $\times$ random points	0.240	*
	<i>P. basiramia</i> $\times$ <i>P. robusta</i>	0.083	
Height of nearest shrub	<i>L. cernua</i> $\times$ random points	0.064	
	<i>L. deckertii</i> $\times$ random points	0.056	
	<i>L. cernua</i> $\times$ <i>L. deckertii</i>	0.113	*
	<i>P. basiramia</i> $\times$ random points	0.052	
	<i>P. robusta</i> $\times$ random points	0.138	*
	<i>P. basiramia</i> $\times$ <i>P. robusta</i>	0.097	

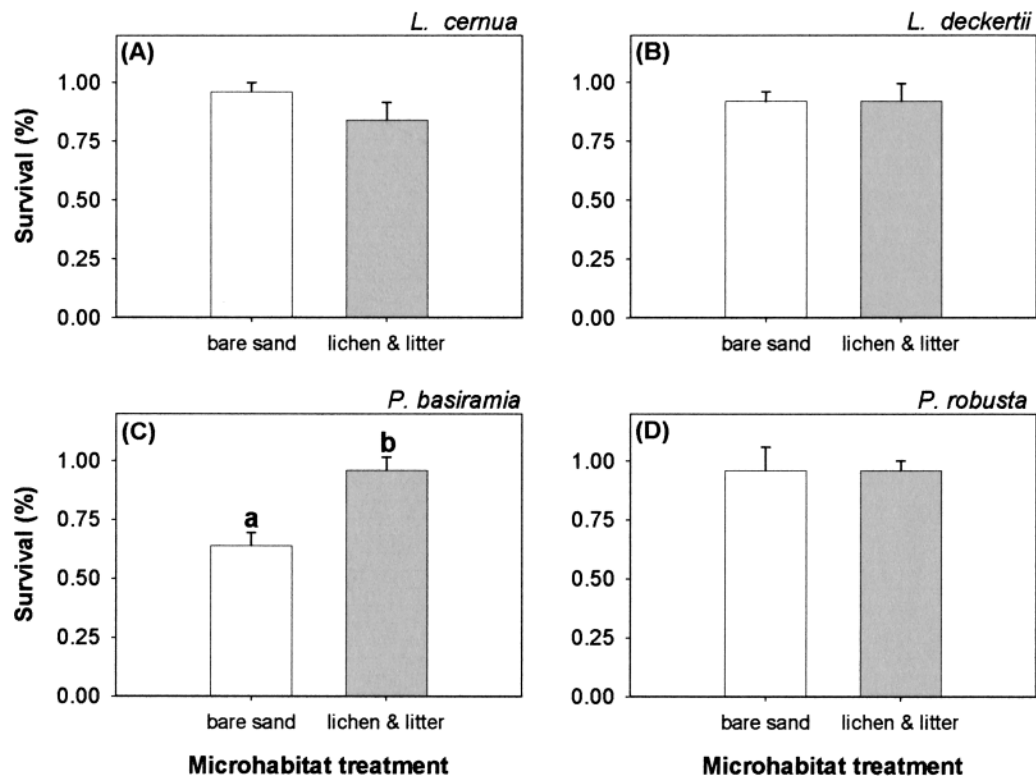


Fig. 2. Means and standard errors of percentage survival of (A) *Lechea cernua*, (B) *L. deckertii*, (C) *Polygonella basiramia*, and (D) *P. robusta* in manipulated soil surface treatments (bare sand vs. lichens and litter added to 100% coverage). Significant differences at  $P < 0.05$  are designated with different letters. Results of logistic regression analyses are shown in Table 2.

TABLE 2. Results of logistic regressions to examine the effects of soil surface microhabitat treatment (bare sand vs. lichen and litter covered) on seedling survival of *Lechea cernua*, *L. deckertii*, *Polygonella basiramia*, and *P. robusta* in rosemary scrub habitat. Initial seedling height is included as a covariate to control for its effect. Means of survival for each species by microhabitat treatment are shown in Fig. 2.

Species	Source	N	Wald $\chi^2$	df	P
<i>Lechea cernua</i>	Microhabitat	50	1.8141	1	0.1780
	Initial height		0.3945	1	0.5299
<i>Lechea deckertii</i>	Microhabitat	50	0.0002	1	0.9891
	Initial height		0.2827	1	0.5950
<i>Polygonella basiramia</i>	Microhabitat	50	5.5717	1	0.0183
	Initial height		0.0360	1	0.8494
<i>Polygonella robusta</i>	Microhabitat	50	0.0006	1	0.9799
	Initial height		1.3984	1	0.2370

*deckertii* and *P. robusta*; however, final seedling size was greater in bare sand microhabitats than in lichen and litter covered microhabitats for the two specialists, *L. cernua* and *P. basiramia* (Fig. 3, Table 3). This difference was significant at the  $P < 0.05$  level for *L. cernua* (Fig. 3A, Table 3), and marginally significant ( $P < 0.1$ ) for *P. basiramia* (Fig. 3C, Table 3).

**Microhabitat and time-since-fire**—Microhabitat characteristics for random points in rosemary scrub habitat change with time-since-fire. As time-since-fire increases, percentage cover

TABLE 3. Results of ANOVAs to examine the effects of soil surface microhabitat treatment (bare sand vs. lichen and litter covered) on final plant size (measured as volume of an inverted cone) of *Lechea cernua*, *L. deckertii*, *Polygonella basiramia*, and *P. robusta* in rosemary scrub habitat. Initial seedling height is included as a covariate to control for its effect. Least squares means of final size adjusted for effects of initial height are shown in Fig. 3.

Species	Source	F	df	P
<i>Lechea cernua</i>	Microhabitat	4.87	1, 42	0.0328
	Initial height	10.30	1, 42	0.0026
<i>Lechea deckertii</i>	Microhabitat	0.61	1, 43	0.4395
	Initial height	3.08	1, 43	0.0862
<i>Polygonella basiramia</i>	Microhabitat	2.93	1, 37	0.0951
	Initial height	4.41	1, 37	0.0426
<i>Polygonella robusta</i>	Microhabitat	0.03	1, 45	0.8667
	Initial height	35.81	1, 45	<0.0001

of bare sand decreases (Fig. 4A), density of *Ceratiola* increases (as measured by shorter distance to nearest *Ceratiola*) (Fig. 4B), density of *Quercus* does not change (Fig. 4C), and neighboring shrub heights increase (Fig. 4D).

**Physical characteristics of microhabitats**—Soil temperatures were affected by microhabitat. Bare sand microhabitats had significantly lower minimum temperatures than lichen and litter covered microhabitats, but maximum temperatures were similar with respect to sand surface treatment (Fig. 5A, Table 4). Microhabitats greater than 2 m from the nearest *Ceratiola*

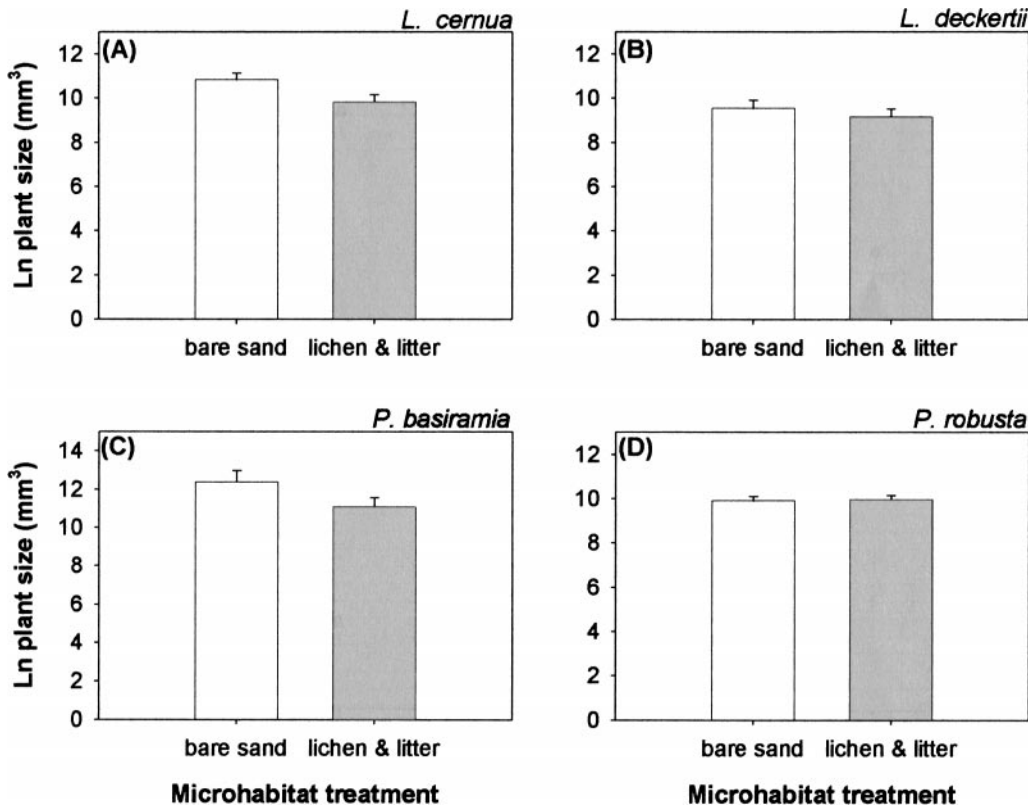


Fig. 3. Final plant size of (A) *Lechea cernua*, (B) *L. deckertii*, (C) *Polygonella basiramia*, and (D) *P. robusta* seedlings in manipulated soil surface treatments (bare sand vs. lichens and litter added to 100% coverage). Least squares means of final size (measured as natural log-transformed volume of an inverted cone) that were adjusted for effects of initial height are shown with standard errors. Means that are significantly different at  $P < 0.05$  are designated with different letters. Results of ANOVAs are shown in Table 3.

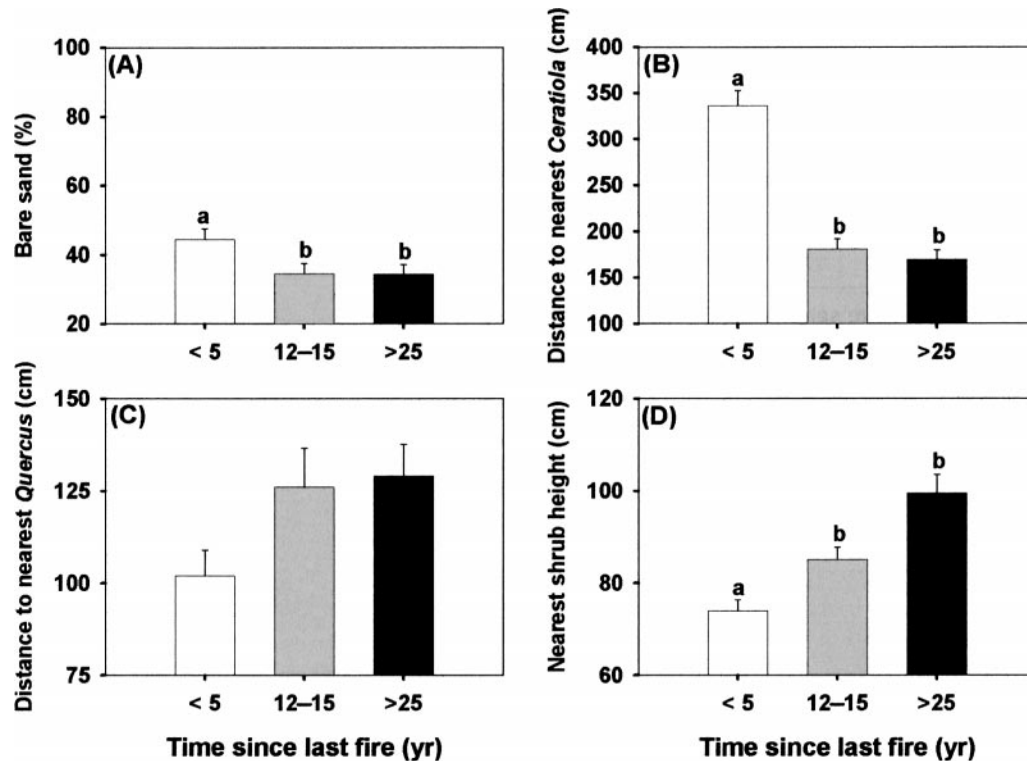


Fig. 4. Means and standard errors of four microhabitat variables, (A) percentage cover of bare sand, (B) distance to nearest *Ceratiola*, (C) distance to nearest *Quercus* spp., and (D) height of nearest shrub, for random points in rosemary scrub habitat patches of three different time-since-fire classes. Bars with the same letter are not significantly different at  $P < 0.017$  (Kruskal-Wallis).

had higher maximum temperatures than microhabitats under the dripline of *Ceratiola*, but similar minimum temperatures (Fig. 5B, Table 4). We found no significant interactions between sand surface treatment and distance from *Ceratiola*; therefore, we present models with main effects only (Table 4).

Percentage soil carbon was lowest in bare sand microhabitats, but similar among other types of microhabitats (Fig. 5C). There was no difference in soil carbon with respect to time-since-fire (Fig. 5D). We found no significant interactions between microhabitat and time-since-fire; therefore, we present models with main effects only (Table 4). Total soil nitrogen was highly correlated with soil carbon ( $r = 0.892$ ,  $P < 0.0001$ ), and the effects of microhabitat and time-since-fire on soil nitrogen were similar to their effects on soil carbon and are not shown. Total soil nitrogen in all samples was low (overall mean = 0.02%).

Soil moisture levels were lower near *Ceratiola* than the other microhabitats, which were similar (Fig. 5E, Table 4). Time-since-fire did not affect soil moisture levels (Fig. 5F, Table 4). We found no significant interactions between microhabitat and time-since-fire; therefore, we present models with main effects only (Table 4).

## DISCUSSION

Percentage cover of bare sand most consistently differed between the rosemary scrub specialists and the habitat generalists, for both congeneric pairs. Although percentage bare sand was correlated with the distribution of all species, the rosemary scrub specialists were significantly more likely to occur in sites with high percentage bare sand, whereas micro-

habitats of generalists were more variable with respect to percentage bare sand. These results are consistent with the results of Hawkes and Menges (1996), who found that the densities of *L. cernua* and *P. basiramia* were higher in patches with a greater percentage of bare sand. Two additional rosemary scrub specialist species, *Hypericum cumulicola* and *Eryngium cuneifolium*, had higher survival in microhabitats with less ground lichen and litter cover (Menges and Kimmich, 1996; Quintana-Ascencio and Morales-Hernandez, 1997). Other studies have also found that characteristics of microhabitat, such as bare ground and soil texture, are critical requirements for the occurrence of particular locally rare species. In a study of microhabitat requirements for seedling establishment in old fields, Gross and Werner (1982) found that two old field species could establish only in 1-yr-old fields where bare ground was abundant, and were not present in 15-yr-old fields where bare ground patches were rare. In a microhabitat manipulation study, Bruno (2002) found that the abundances of three locally rare annual cobble beach plant species were limited by scarcity of their required microhabitat, fine-grained sands with low tidal flow velocity.

Plants of both rosemary scrub specialists and habitat generalists occurred less frequently near neighboring shrubs, *Ceratiola* and *Quercus* spp., than random points. Our results, and those of Menges and Kimmich (1996) and Quintana-Ascencio and Morales-Hernandez (1997), suggest that *Ceratiola ericoides* has an inhibitory effect on both rosemary scrub specialist species and habitat generalists. *Ceratiola ericoides* has been shown to have allelopathic effects on pines and grasses of sandhills (Richardson and Williamson, 1988) as well as on

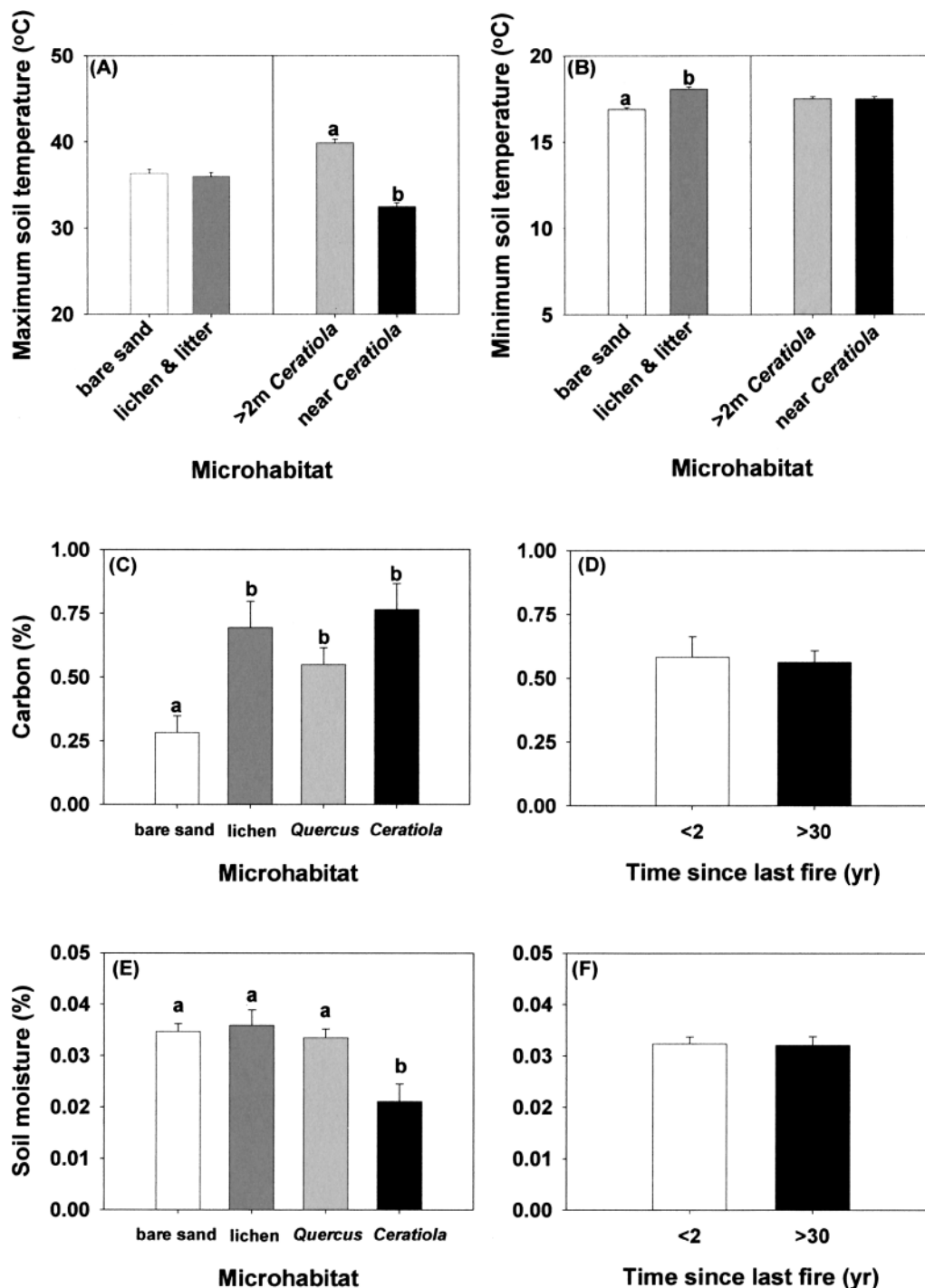


Fig. 5. Means and standard errors of (A) and (B) soil temperature, (C) and (D) percentage soil carbon, and (E) and (F) percentage soil moisture with respect to (A, B, C, E) microhabitat and (D, F) time-since-fire. For the soil temperature study, there were two levels of the soil surface cover treatment (lichens and litter added vs. bare sand) and two levels of distance from nearest *Ceratiola* (near *Ceratiola* vs. >2 m from nearest *Ceratiola*). For the total carbon and soil moisture study, there were four levels of microhabitat, (1) bare sand, 2 m from *Ceratiola*, and 1 m from *Quercus*; (2) lichens and litter at >90% cover, 2 m from *Ceratiola*, and 1 m from *Quercus*; (3) under the dripline of *Quercus*; and (4) under the dripline of *Ceratiola*, and two levels of time-since-fire (<2 yr since last fire vs. >30 yr since last fire). Means that are significantly different at  $P < 0.05$  are designated with different letters. ANOVA results are shown in Table 4.

several perennial herb species that occur in rosemary scrub, including rosemary scrub specialists and habitat generalists (Hunter and Menges, 2002). Our results suggest that the same may be true for all four species included in our study. We also

found that soil moisture was significantly lower in microhabitats near *Ceratiola* shrubs, in comparison to other microhabitats. The combined effects of allelopathy and reduced soil moisture may make microhabitats near *Ceratiola* difficult to

TABLE 4. Summary of ANOVAs to examine the effects of microhabitat variables and time-since-fire on soil properties in rosemary scrub habitat. In the soil temperature study, there were two levels of the soil surface cover treatment (lichens and litter added or bare sand) and two levels of distance from nearest *Ceratiola* (near *Ceratiola* and >2 m from nearest *Ceratiola*). In the total carbon and soil moisture study, there were four levels of microhabitat (bare sand, lichens and litter at >90% cover, under the dripline of *Quercus*, and under the dripline of *Ceratiola*) and two levels of time-since-fire (<2 yr since last fire and >30 yr since last fire). Means are shown in Fig. 5.

Soil variable	Treatment	F	df	P
Maximum temperature	Soil surface cover	0.29	1, 17	0.5962
Maximum temperature	Distance from <i>Ceratiola</i>	122.54	1, 17	<0.0001
Minimum temperature	Soil surface cover	47.31	1, 17	<0.0001
Minimum temperature	Distance from <i>Ceratiola</i>	0.00	1, 17	0.9546
Percentage total carbon	Microhabitat	6.86	3, 31	0.0011
Percentage total carbon	Time-since-fire	0.05	1, 31	0.8210
Percentage soil moisture	Microhabitat	8.137	3, 55	<0.0001
Percentage soil moisture	Time-since-fire	1.806	1, 55	0.1850

colonize for many perennial herbs that occur in rosemary scrub. With the exception of the habitat generalist, *L. deckertii*, plants occurred less frequently near *Quercus* shrubs than random points. Competition from *Quercus* spp. did not substantially affect survival and growth of transplanted seedlings of three rosemary scrub specialists in a field experiment (Quintana-Ascencio and Menges, 2000); however the favorable growing conditions during that study due to high rainfall associated with El Niño may have reduced differences between microsites near to and far from *Quercus* spp. Our study occurred during a drought year; competitive effects of *Quercus* on perennial herbs are likely to be most noticeable during low rainfall years.

Bare sand microhabitats may be critical to seed and seedling life history stages of rosemary scrub specialist species, which would support the narrower regeneration niche hypothesized as the mechanism of specialization. In contrast to Quintana-Ascencio and Menges (2000), we found that seedling survival was higher in the presence of ground lichens and litter for *P. basiramia*. They monitored both germination and seedling establishment of *P. basiramia* in microsites with and without the presence of ground lichens; we measured the effects of ground lichens and litter on seedling survival after seedlings had already established. Ground lichens and litter may have negative effects on seedling germination and establishment (Hawkes and Menges, 2003), but not survival after seedlings reach a critical size. We also found that seedlings of the two rosemary scrub specialist species grew larger in the absence of lichens and litter, although these differences in growth were not dramatic. Seedling growth is one of the most important life history parameters for population growth of another rosemary scrub specialist species, *Eryngium cuneifolium* (Menges and Quintana-Ascencio, 2004) and is expected to be a critical life history parameter for *L. cernua* and *P. basiramia*, in part because these species are short-lived (Maliakal-Witt, unpublished data). Thus, greater germination rates, seedling establishment, and seedling growth of these rosemary scrub specialists in bare sand may be significant in determining their strong tendency to occur in these types of microhabitats.

As time-since-fire increases, microhabitat characteristics in rosemary scrub habitat become less suitable for rosemary scrub specialist species. *Ceratiola* shrubs become denser and all shrubs become taller as time-since-fire increases (Abrahamson, 1984a; Quintana-Ascencio and Morales-Hernandez, 1997; Schmalzer, 2003; this study). Fires eliminate adult *Ceratiola* shrubs, and new individuals establish slowly from seed (Menges and Kohfeldt, 1995). However, *Quercus* species resprout

quickly following fire (Abrahamson, 1984b; Menges and Kohfeldt, 1995) and recruitment events are not associated with fires, but rather annual precipitation and masting years (Abrahamson and Layne, 2002; Abrahamson and Layne, 2003). Therefore, it is not surprising that *Quercus* density did not change with time since fire. Percentage cover of bare sand decreases with time since fire, as ground lichens and leaf litter increase in cover (Menges and Kohfeldt, 1995; Hawkes and Menges, 1996; and this study). Thus fires can help maintain suitable microhabitats for rosemary scrub specialist herbs by reducing competition from *Ceratiola ericoides* and exposing bare sand microsites for seedling establishment. Frequent fires increase the population viability of *Hypericum cumulicola* and *Eryngium cuneifolium*, two rosemary scrub specialist herbs (Quintana-Ascencio et al., 2003; Menges and Quintana-Ascencio, 2004). Management agencies can assess the benefits of prescribed fires for rosemary scrub specialist species by post-fire monitoring of the availability of bare sand microhabitats that are free from competition from neighboring *Ceratiola*.

The differences in physical characteristics of microhabitats we measured do not fully account for the tendency of rosemary scrub specialists to occur in bare sand microhabitats. Although soils near *Ceratiola* had lower soil moisture levels than other types of microhabitats, soils near *Quercus* do not have lower soil moisture levels than microhabitats greater than 2 m from any neighboring shrub, which suggests that *Quercus* may have less of a competitive effect than *Ceratiola*. D. Gagnon et al. (University of Quebec at Montreal, unpublished manuscript) also found that *Ceratiola* has a much greater effect on soil moisture availability than *Quercus* species. Among the variables we measured, bare sand microhabitats can be distinguished from the other types of microhabitats only by lower minimum temperatures and total soil carbon. The magnitude of the temperature difference is small, about 1°C, which is unlikely to produce ecologically meaningful differences in metabolic rate (Criddle et al., 1994). Soil carbon content generally is positively correlated with nutrient supply (Madsen and Larsen, 1997). Greater seedling growth in bare sand microhabitats occurs despite lower levels of soil carbon and nitrogen. Other biotic characteristics also may affect seedling establishment and growth, such as cryptogamic soil crusts (Hawkes and Flechtner, 2002).

In conclusion, our results support the hypothesis that habitat specialists occur in a narrower range of microhabitat conditions than species that occur in a broader range of habitats. Previous studies have demonstrated the importance of micro-

habitat for the persistence of individual geographically restricted, rare species (Griffith, 1996; Hilton and Boyd, 1996; Menges and Kimmich, 1996; Kephart and Paladino, 1997; Dinsdale et al., 2000; Wolf, 2001; Colling et al., 2002). Other studies have shown that the local distributions of geographically widespread, but locally rare species are determined by availability of suitable microhabitat (Platt, 1975; Gross and Werner, 1982; Bruno, 2002). Our comparison of two sympatric pairs of habitat-specialist and habitat-generalist congeners suggests that microhabitat specialization may underlie habitat specificity. In this case, the limited amount of rosemary scrub habitat that also contains sufficiently high levels of bare sand appears to directly restrict the distributions of *L. cernua* and *P. basiramia*. Rosemary scrub habitat is characterized by large gaps lacking shrubs, and a high percentage of bare sand (Menges, 1999). In neighboring scrubby flatwoods and sandhill habitats, gaps are less common, smaller, less persistent, and contain less percentage bare sand than gaps in rosemary scrub (Abrahamson et al., 1984; Menges and Hawkes, 1998). These differences in microhabitat availability among habitat types may preclude the occurrence of rosemary scrub specialists in other habitats because they can only persist in a narrow range of microhabitat conditions with high levels of bare sand. Conversely, the generalist species can tolerate a wider range of variation in lichen and litter cover, including and exceeding the range of microhabitats preferred by rosemary scrub specialists. As a result, the generalist species can occur in multiple habitat types, and thus over a larger geographic area. Consideration of habitat specificity, microhabitat requirements, and microhabitat distribution is needed for appropriate management of rare species. If habitat-specialist species are also specialized on particular microhabitat features within their preferred habitat, they may be more vulnerable to extinction than can be predicted by their degree of habitat specificity alone.

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